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ON THE DETAILED SKULL STRUCTURE OF A CRESTED HADROSAURIAN DINOSAUR

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A partial skeleton of a crested hadrosaurian dinosaur, collected by the Smithsonian Paleontological Expedition of 1928, is unique in having the occipital region of the skull disarticulated, thus displaying structural features not before observed in the Hadrosauridae. The specimen (U.S.N.M. no. 11893) comes from the Two Medicine formation of the Upper Cretaceous and was found by G. F. Sternberg on the north side of the Two Medicine River, Blackfeet Indian Reservation, Teton County, Mont. Although a considerable part of the skeleton was recovered, it is only the skull parts with which we are now concerned.

That this specimen pertains to the subfamily Lambeosaurinae is clearly indicated by the reduced number of vertical rows of teeth in the dentaries, the deep and nearly vertical suture between the frontal and nasal bones for the better anchorage of the crest, and the short, broad nature of the cerebral expansion of the brain as indicated by the frontal contribution to the brain case.

The lack of the crest portion of the skull and the juvenile character of the present individual make it very difficult if not impossible to identify this specimen generically at this time.

The detailed osteological structure of the occipital segment is the least-known part of the hadrosaurian skull, for in most crania the sutures are coalesced, thus obscuring or hiding entirely the precise extent of the individual elements.

The present specimen, therefore, appears worthy of the detailed description that follows:

Parietal.—The coalesced parietals are much constricted between the supratemporal fossae, the posterior half presenting a thin median crest that rises to the level of the superior squamosal border. The anterior half is rounded transversely and widely expanded at the end, where it is in sutural contact with the whole posterior ends of the frontals and appears to meet the postfrontal on its outer anterior angle. At the center a broad rounded median prolongation is interposed between the frontal bones, as in *Lambeosaurus*. Posteriorly the slightly widened end of the parietal overhangs the supraoccipital and is suturally joined to the squamosals on either side. This end is visible from a posterior view, as in *Cheneosaurus* (see fig. 30). Ventrally the parietal sits astride the supraoccipital with which it is closely joined on the two sides (see fig. 29); anterior to the supraorbital it unites ventrally with the alisphenoid, but nowhere is it in contact with the prootic or the exoccipital, although Lambe was of the opinion that both of these bones articulated with the parietal in *Edmontosaurus*. He was certainly wrong in regard to the exoccipital, for I do not know of any dinosaurian skull in which these two bones are in contact.

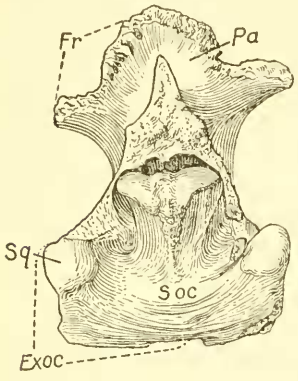

FIGURE 29.—Parietal (lacking posterior end) and supraoccipital (U.S.N.M. no. 11893), posterior view. *Exoc.*, sutural border for the exoccipital; *Fr*, sutural border for the frontal; *Pa*, parietal; *Soc*, supraoccipital; *Sq*, articular surface for squamosal articulation. One-half natural size.

MEASUREMENTS OF PARIETAL

Greatest length along midline	71 mm
Greatest width across anterior end	66 mm
Greatest width across posterior end	15 mm

Supraoccipital.—The supraoccipital was found articulated with the overlying parietal, as shown in figure 29. Viewed posteriorly the supraoccipital is a subtriangular, blocklike bone that is enclosed above by the parietals and squamosals and that is in contact below with the exoccipitals. The broad, rounded, bilobed upper surface of the median crest of this bone is smooth and gives no indication of sutural union with the overlying parietal. It was evidently a cartilaginous union such as is commonly found in the Sauria. A similar condition exists in *Camptosaurus* and *Stegosaurus*. In aged individuals this surface may become coossified with the parietal, as is known to be the case in *Stegosaurus*. On either side well below the crest these two

bones meet in grooved sutural contact. Ventrally the supraoccipital presents two sutural surfaces that articulate with the exoccipitals. The posterior one is horizontal, the anterior face oblique looking outward, forward, and downward. On the posterolateral angles of this bone are raised smoothly rounded protuberances that look upward and articulate with a cupped surface developed on the lower border of the squamosal, as shown in figure 30. This rounded articular surface is contributed to laterally by the exoccipital.

This is a most unusual cranial articulation that gives every indication of being a movable union, although the other articulating surfaces of both squamosal and supraoccipital are through the medium of roughened sutural contacts. This ball and socket articulation may be present in all hadrosaurian cranii, but through coalescence no trace of such a union has before been observed in this family or for that matter in other dinosaurian skulls. The ventral side of the supraoccipital, although slightly excavated at the center (see fig. 29), presents a continuous roughened sutural surface across the entire width of the bone, indicating that the exoccipitals meet on the median line and thus exclude the supraoccipital from participation in the boundary of the foramen magnum, as in *Bactrosaurus*.[1] This inward median extension of the one exoccipital bone present is broken off, so one has to rely on the continuous sutural surface as evidence of the condition described above, although corroborative evidence is furnished by the cross section of a skull figured by Brown,[2] which shows the exoccipital below the supraoccipital on the midline above the foramen magnum. This is a structural modification known at this time only in the hadrosaurian skull among the Dinosauria. Anteriorly the supraoccipital is deeply excavated, thus forming the posterior portion of the brain case. A heavy triangular-shaped sutural surface on the anterior border that looks forward and outward is the contact for the prootic.

MEASUREMENTS OF SUPRAOCCIPITAL

Greatest length	52 mm
Greatest transverse width	65 mm
Greatest vertical depth	42 mm

Squamosal.—The squamosals are separated on the median line by the interposition of a backwardly extended process of the parietal, which they meet by a strongly ridged and grooved suture. They are only 10 mm apart (see fig. 30). This union with the parietal continues downward and forward on either side of the upper median part of the supraoccipital. Ventrally it unites with the supraoccipital by a smooth cupped articulation, which rests upon the ball-like

[1] Gilmore, Charles W., Bull. Amer. Mus. Nat. Hist., vol. 67, p. 55, fig. 22, 1933.
[2] Brown, Barnum, Bull. Amer. Mus. Nat. Hist., vol. 33, pl. 36, 1914.

protuberance on the supraoccipital, to which the exoccipital contributes an outer portion. This articulation has been more fully described in connection with the supraoccipital. External to this cup the squamosal sends downward and outward a narrow, compressed, tapering process. In the articulated skull this process is closely applied posteriorly, especially at its upper end, to the paraoccipital process of the exoccipital, and they continue in apposition throughout their lengths.

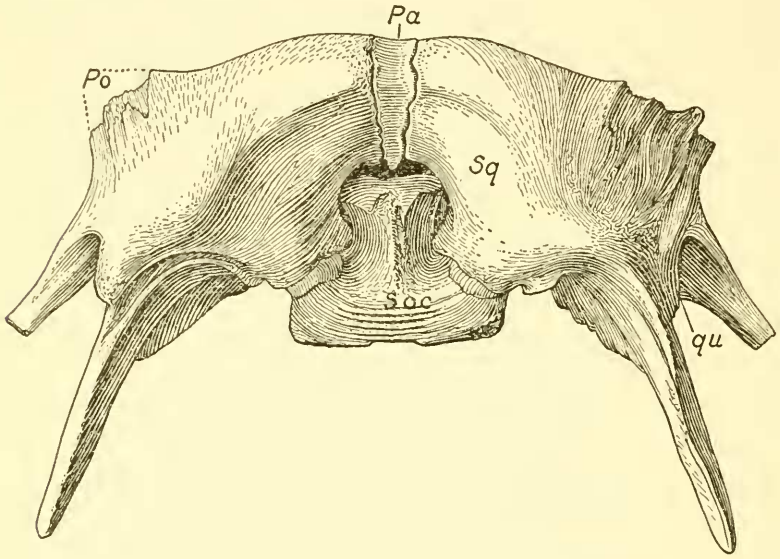

FIGURE 30.—Articulated squamosal, parietal, and supraoccipital (U.S.N.M. no. 11893). *Pa*, parietal; *qu*, cotylus for the quadrate; *Po*, sutural surface for articulation of postorbital; *Soc*, supraoccipital; *Sq*, squamosal. One-half natural size.

From a lateral aspect the squamosal presents a wide surface between its upper border and the top of the cotylus for the head of the quadrate. This is a peculiarity distinctive of all known members of the Lambeosaurinae, as the other members of the Hadrosauridae are relatively narrow in this view. The cotylus is deep. A pointed process of moderate length extends downward from its anterior border lapping along the front of the quadrate. Above and anterior to this process the squamosal is a short tapering process that unites by squamous union with the inner side of the postfrontal. The posterior overlap of the postfrontal is Y-shaped with the ventral branch much longer than the upper, as indicated by the sutural surfaces on the exterior surface of the squamosal. This same condition is found in *Lambeosaurus*, *Corythosaurus*, and *Saurolophus*.

MEASUREMENTS OF SQUAMOSAL

Length from posterior border to anterior termination beneath the postfrontal	80 mm
Breadth from parietal contact, obliquely outward and downward to end of external process	150 mm
Depth from supratemporal fossa border to rim of cotylus	52 mm

Exoccipital.—Only the left exoccipital is present, but it is in excellent preservation, as shown in figure 31. The exoccipital contributes extensively to the formation of the occipital condyle; a heavy posterior projection contributes nearly one-third of the complete condyle. The inferior horizontal surface unites with the basioccipital by a coarsely roughened sutural surface. Internally the surface is concave dorsoventrally forming the lateral boundary of the foramen magnum. This portion of the exoccipital is perforated by two foramina, which pass diagonally through the bone. The larger and more posterior is for the passage of the twelfth or hypoglossal nerve; the smaller anterior one for the eleventh or accessory nerve. The upper portion of the exoccipital has been described in connection with the supraoccipital.

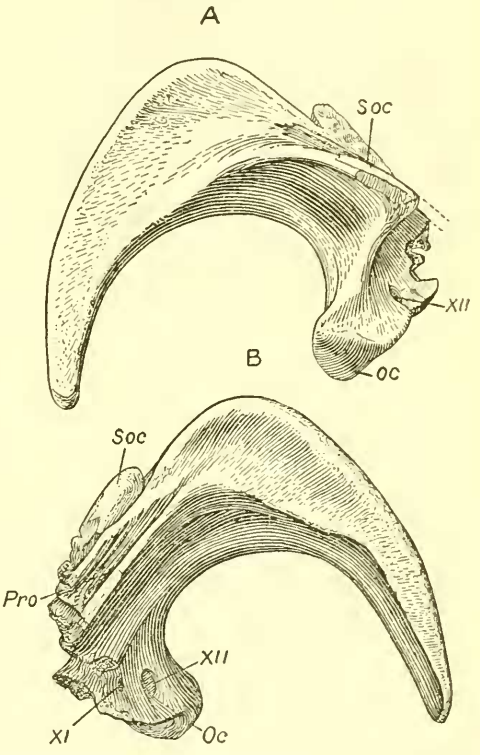

FIGURE 31.—Left exoccipital (U.S.N.M. no. 11893): A, Posterior view; B, anterior view. *Oc*, exoccipital contribution to the occipital condyle; *Pro*, sutural surface for union of prootic; *Soc*, articulating surface for union with the supraoccipital; *XI* and *XII*, foramena for the eleventh and twelfth nerves. One-half natural size.

The outer portion of this bone extends outward and backward and develops a large hooked paraoccipital process that in position lies against the squamosal process, which it supports and resembles in general shape. Its bluntly pointed extremity extends below that of the squamosal. On the inner end of the anterior side below the articulation of the supraoccipital a grooved subtriangular surface marks the union with the prootic (see fig. 31, B, *Pro*).

Frontals.—The coossified frontal bones are shown in figure 32. The frontals are of the typical Lambeosaurinae type; that is, much reduced in length, wider than long, and with a deep nearly vertical sutural surface for union with the nasals. This sutural area is nearly

one and one-half times the length of the dorsal surfaces of the frontals. It serves as a strong anchorage for the crest, which is missing in this specimen.

On the posterior border at the center the nasals are notched for a median forward projection of the parietal, but less deeply than in *Lambeosaurus*.[3] The ventral view (fig. 32, B) shows the very short but wide contribution to the brain case in which the cerebral portion of the brain was lodged. This feature is peculiar to the crested hadrosaurs and much unlike the elongate compressed cerebrum of *Thespesius*, *Edmontosaurus*, and presumably all non-crested forms of the Hadrosauridae.

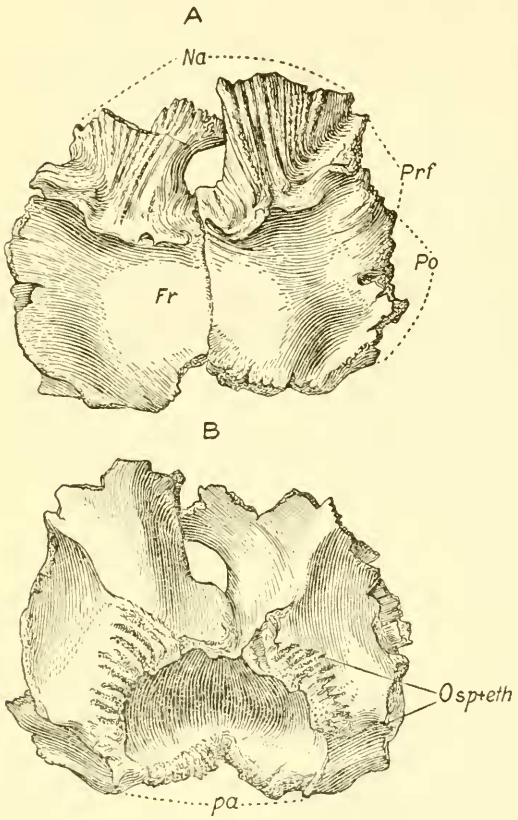

FIGURE 32.—Articulated frontal bones (U.S.N.M. no. 11893): A, Superior view; B, ventral view. *Fr*, frontal; *Na*, sutural surface for articulation of nasals; *Osp+eth*, sutural border for orbitosphenoid and ethmoid; *Pa*, sutural border for parietal; *Po*, sutural border for postorbital; *Prf*, sutural border for prefrontal. One-half natural size.

The lateral borders are in contact throughout their whole length with the prefrontal and postorbital, as shown in figure 32, and thus do not contribute to the formation of the orbital rim, as they do in the crestless hadrosaurs.

The illustration shows the bone as it is preserved, with a large foramen at the middle of the sutural slope. I am of the opinion that the left frontal has been crushed inward against the right element and that in the normal state there would be a deep gap between these two elements at this point. In *Lambeosaurus* there is a wide open notch.

MEASUREMENTS OF FRONTALS

Greatest length dorsal surface on median line	39 mm
Greatest width	107 mm
Depth of nasal suture	48 mm
Length of brain case	30 mm
Width of brain case	55 mm

[3] Gilmore, Charles W., Geol. Surv. Canada Bull. 38, p. 37, fig. 8, 1924.

Postorbital.—The element here designated postorbital is usually called postfrontal by authorities. It may represent a complex of these two elements, as in the theropodous dinosaurs, but in the present instance the alisphenoid articulates with it on the internal side, being received in a depression or pit. In those dinosaurian skulls in which prefrontal, postfrontal, and postorbital bones can be distinctly recognized, this cupped depression for the alisphenoid is always on the inner side of the postorbital bone, and it is largely for that reason that it is so designated here.

The postorbital has the usual triradiate form. Its posterior extension overlaps by squamous union the forward extension of the squa-

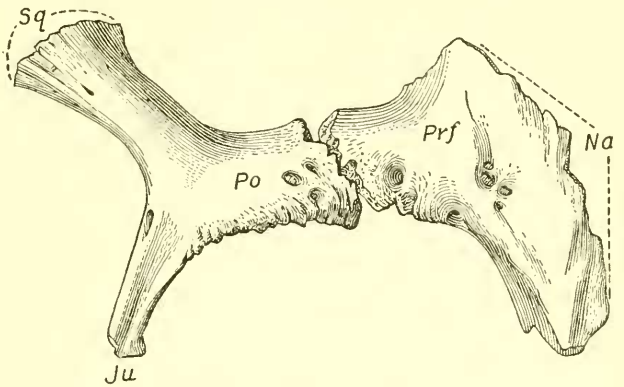

FIGURE 33.—Articulated postorbital and prefrontal bones (U.S.N.M. no. 11893), lateral view. *Ju*, Process that unites with jugal; *Na*, inner side in contact with the nasal; *Po*, postorbital; *Prf*, prefrontal; *Sq*, process that unites with the squamosal. One-half natural size.

mosal and forms the supratemporal arcade separating the supratemporal from the infratemporal fossa. The posterior end is expanded dorsoventrally and on the inner side is deeply excavated for the squamosal process, which extends forward the full length of this bar. The anteriorly directed process is in contact internally by a zigzagged suture with the frontal for half its length. The heavy anterior end unites by suture with the prefrontal above the center of the orbit, as shown in figure 33. The descending bar, which is trihedral in cross section, united with an ascending process of the jugal by squamous union to form the postorbital bar. On the inner side at the junction of the three rays is a shallow rounded depression for the articulation of the outer end of the alisphenoid.

Prefrontal.—The prefrontal completes the upper border of the orbit articulating behind with the postorbital and in front with the lachrymal. Its upward extension is very thin and lapped the base of the elevated crest formed by the nasals as in *Cheneosaurus*. With the postorbital it excludes the frontal participation in the orbital rim, a peculiarity of the crested hadrosaurs, whereas in most of the crestless

forms it comprises a small portion of the border. The characteristic shape of this bone is well shown in figure 33.

Prootic.—Both disarticulated prootic bones are present, the left element in excellent preservation. The bone here called prootic in all probability represents the coossified prootic, epiotic, and opisthotic, certainly the last, for as in most reptiles these probably fused early in life, and thus all trace of their sutural junctions has long since been obliterated.

The prootic lies posterior to the alisphenoid and anterior to the exoccipital. Above it is in contact with the supraoccipital, below with the basisphenoid. In *Edmontosaurus*, Lambe [4] shows the prootic in contact with the parietal, and likewise Brown [5] in a trachodont brain case described by him found this complex in contact with the parietal. A similar condition exists in the crocodile skull. However, in the skull under consideration they are distinctly separated by the interposition of portions of the supraoccipital and alisphenoid bones. The pointed posterior half of this complex, probably the opisthotic portion on the inner side, presents two longitudinally ridged and grooved sutural surfaces, the upper one uniting with the supraoccipital, the lower with the exoccipital. This side is about equally divided between the two bones and overlaps the junction of the supraoccipital and exoccipital. The prootic proper is perforated by the foramen for the seventh or facial nerve. The anterior border is deeply notched by the foramen ovale for the fifth or trigeminal nerve, but the portion carrying the foramen for the eighth or internal auditory meatus is missing, and its position cannot be accurately determined in this specimen.

Alisphenoid.—The alisphenoid has the usual triangular curved form and lies in front of the prootic and bounds the large foramen for the trigeminal nerve in front. It connects superiorly with the parietal and frontal. The outer rounded end is received in a pit on the upper inner surface of the postfrontal+postorbital complex. This bone forms the wall of the brain case, which lodges the cerebral hemispheres.

The division between the alisphenoid and prootic is marked by a suture that descends from the floor of the supratemporal fossa and enters the foramen ovale forward of the upper curve of that opening. The external surface forms a part of the inner and anterior boundaries of the supratemporal fossa. A narrow groove on the external surface extending forward from the foramen ovale was for the reception of the ophthalmic branch of the fifth nerve. In form and relationships with surrounding elements this alisphenoid is in full accord with the conditions found in other hadrosaurian skulls. Anteriorly

[4] Lambe, L. M., Geol. Surv. Canada Mem. 120, p. 17, fig. 26, 1920.
[5] Brown, Barnum, Bull. Amer. Mus. Nat. Hist., vol. 33, pl. 36, 1914.

it unites with the orbitosphenoid, but their precise relationships are not clearly shown by this specimen.

Orbitosphenoid.—A pair of small subrectangular bones (see fig. 34, *Osp*) are identified as the orbitosphenoids. This identification rests to a considerable extent on the presence of several foramina that perforate these bones and that can be homologized with the nerve openings in the orbitosphenoid region in other Dinosauria crania. Unfortunately, the sutural edges have suffered from abrasion and crushing and thus offer little positive information as to their correct

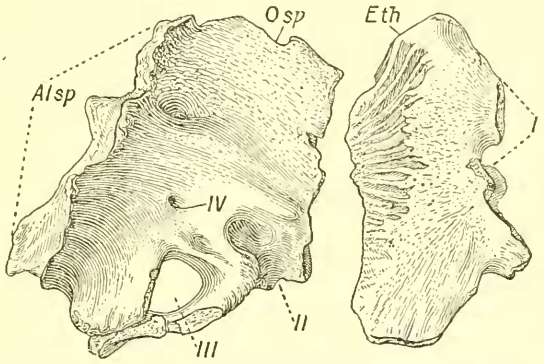

FIGURE 34.—Right orbitosphenoid and ethmoid (U.S.N.M. no. 11893). *Alsp*, sutural border for alisphenoid; *Eth*, ethmoid; *Osp*, orbitosphenoid; *I*, outlet for the olfactory nerve; *II*, the second or optic foramen; *III*, *IV*, foramen for third and fourth cranial nerves, respectively. Natural size.

relationships to the surrounding skull elements. A deeply grooved sutural border, having an extensive outer lip for squamous union, fulfills all requirements for a perfect articulation with the ethmoid and thus is regarded as the anterior edge of this bone. The superior edge is especially thickened for articulation with the overlying frontal. The posterior unites with the alisphenoid, and the ventral with the basioccipital, which is missing in this specimen. Since the basisphenoid and parasphenoid are both missing, it cannot be determined whether the orbitosphenoid was in contact with the parasphenoid. A small triangular sutural area on the lower anterointernal side of the orbitosphenoid appears to indicate a surface for union with its fellow of the opposite side on the median line below the forward part of the cerebral hemispheres.

The orbitosphenoid is perforated by a number of foramina identified as shown in figure 34.

The foramen for the optic nerve lies very close to the orbitosphenoid-ethmoid sutural border, and in this specimen it seems to be a notch or groove on the anterior ventral border of the orbitosphenoid with the ethmoid contributing to its boundary. It is quite possible that in better-preserved specimens an external view would

show the foramen as entirely enclosed within the orbitosphenoid bone.

Posterior to the optic foramen and separated by a wall of bone 8 mm in width is the foramen for the third nerve (see fig. 34). Immediately above the foramen for the third nerve are two small foramina one above the other. On the external surface a short shallow groove runs forward from each of these openings. It seems quite probable that the most ventral gave exit to the fourth or trochlear nerve. The superior one may have transmitted a blood vessel. On the ventral posterior border of the orbitosphenoid there is a shallow groove leading down to the sutural border which in the articulated skull may have led to the foramen for the abducent or sixth cervical nerve.

MEASUREMENTS OF ORBITOSPHENOID

Greatest length, anteroposteriorly	34 mm
Greatest height, dorsoventrally	48 mm

Ethmoid.—A pair of small subrectangular elements (see fig. 34) are identified as the ethmoids. In adult skulls the suture between the ethmoid and orbitosphenoid becomes so fully coalesced as to leave no trace of their union. In *Tyrannosaurus* Osborn [6] indicated the questionable presence of an ethmoid, and in describing the skull of *Edmontosaurus* Lambe [7] designated the lateral area immediately posterior to the exit of the olfactory nerves as being the presphenoid. In a brain case of *Saurolophus osborni* illustrated by Brown,[8] it now becomes evident, in the light of the present specimen, that the anterior portion of the element designated alisphenoid is the coalesced alisphenoid and orbitosphenoid and that the bone called presphenoid is the ethmoid. Other authors have considered all the brain case between the alisphenoid and exit for the olfactory nerves as being the orbitosphenoid bone. After comparison of the present specimen with the brain case of *Antrodemus*, *Camarasaurus*, *Triceratops*, *Stegosaurus*, *Thespesius*, and *Kritosaurus*, I am of the opinion that the ethmoid, although fused, is present in all these genera and probably in all Dinosauria.

Posteriorly the ethmoid unites with the orbitosphenoid, being received in a groove along the edge of the latter bone, which sends a wide thin process forward for a squamous overlap for one-half the width of the ethmoid, as shown in figure 34. In the left element this external sutural surface covers more than half the width of the bone. The strongly ridged and radiating nature of the suture renders the union of these two elements distinctive and thus contributes to the positiveness of their proper identification. The upper sutural end is widened transversely but constricted anteroposteriorly and thus

[6] Osborn, H. F., Mem. Amer. Mus. Nat. Hist., vol. 1, no. 1, figs. 8, 12, 1912.
[7] Lambe, L. M., Geol. Surv. Canada Mem. 120, p. 47, fig. 26, 1920.
[8] Brown, Barnum, Bull. Amer. Mus. Nat. Hist., vol. 31, p. 134, fig. 3, 1912.

has a limited contact with the frontal. The ventral third gradually thins toward the border with an outward inclination of the whole end. The slightly roughened inner surface of this end apparently indicates its lapping union with the missing parasphenoid. At about midlength on the internal side a low longitudinal ridge evidently marks the ventral limit of the olfactory lobes. Whether these ridges met on the median line, and thus formed the floor of this portion of the brain case, cannot be determined. There is no indication of a median bony septum, such as is present in *Tyrannosaurus*, and it would appear that in this form the ethmoids enclose an undivided cavity for the olfactory lobes of the brain and form an opening leading into the nasal and prenasal cavities in front of the orbits. In *Triceratops*[9] the ethmoidal region roofs over the olfactory lobes of the brain, a condition that could not possibly exist in this specimen.

MEASUREMENTS OF ETHMOID

Greatest length, anteroposteriorly	24 mm
Greatest depth, dorsoventrally	44 mm

SUMMARY

The study of this disarticulated brain case discloses for the first time in the Hadrosauridae the presence of a distinct ethmoid bone; the presence of a semimovable articulation between the squamosal, supraoccipital, and exoccipital; and contributes evidence that in this family the supraoccipital is excluded from participation in the boundary of the foramen magnum.

[9] Hay, O. P., Proc. U. S. Nat. Mus., vol. 36, p. 102, pl. 2, 1909.

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